Appendix B-4. (Cont.)

Original Variable*	Canonical Variable IX	X	XI	XII	XIII	XIV	XV	XVI	XVII
(1) ____	0.31524	–0.29721	–1.35774	1.28042	1.13986	0.15862	–0.34562	–0.32372	–0.58717
(2) ____	0.17348	–0.28305	0.14086	0.05604	–0.02564	–0.14636	–0.06826	0.02907	0.02131
(3) ____	0.52645	–0.35123	–0.35495	–0.44118	0.01969	0.51702	0.14068	0.34130	–0.02324
(4) ____	–0.37768	1.22177	0.12469	–0.24783	–0.13443	0.16893	0.29975	–0.06626	0.06618
(5) ____	0.40608	0.24544	–0.27064	0.20149	–0.00746	–0.14897	0.15740	0.10154	0.00098
(6) ____	0.52460	0.28829	–0.17545	–0.53465	0.23185	–0.17844	–0.28399	–0.03109	0.00954
(7) ____	–2.16480	0.92544	0.04893	0.27989	0.38756	0.21524	–0.28176	0.21978	0.04156
(8) ____	0.38353	0.18608	–1.06463	0.65041	0.31213	0.60648	–0.10383	–0.61341	0.48687
(9) ____	0.27665	0.42594	–0.12355	0.37803	–0.68281	0.04671	–0.31473	0.00488	–0.10144
(10) ____	0.58597	0.07439	0.44295	0.64397	0.06521	–0.33845	–0.10428	0.23671	0.34545
(11) ____	0.09293	0.31406	0.10102	–0.04680	–0.06119	0.19438	0.07421	–0.16847	–0.09627
(12) ____	–0.46265	–0.16144	0.08774	0.02555	–0.09284	–0.39839	–0.11458	–0.08829	0.09041
(13) ____	–1.14325	–0.58947	–1.16856	–0.32804	0.05919	–0.07113	–0.03210	0.22149	0.05686
(14) ____	0.04107	–0.19174	0.33143	–0.12743	0.03399	0.14834	–0.11996	–0.01482	–0.00629
(15) ____	–0.50868	–0.86440	0.36109	0.65656	–0.31980	0.35957	0.20668	0.05680	–0.00422
(16) ____	–0.53148	–0.63765	–0.56559	–0.39705	–0.68591	–0.22037	0.14742	–0.37113	0.01886
(17) ____	–0.54097	0.11446	0.34495	–0.01641	–0.02316	–0.52479	0.16036	0.06695	–0.27026
(18) ____	–0.14053	–0.43373	0.36500	–0.09021	0.80888	–0.15075	0.36403	–0.17839	0.03976

* See Table 1.

Appendix C.—Mean distance matrix for *Marmota*, sexes combined.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1) *M. c. doppelmayeri*	0.								
(2) *M. c. bungei*	4.84632	0.							
(3) *M. c. camtschatica*	6.05310	4.26038	0.						
(4) *M. broweri*	6.13463	5.38503	6.74744	0.					
(5) *M. caligata* ssp. (Alaska, Canada)	8.94952	8.30244	7.95774	6.84412	0.				
(6) *M. c. nivaria*	11.11063	10.44140	10.47773	7.37649	5.73291	0.			
(7) *M. c. cascadensis*	9.62144	8.74978	8.06889	8.36285	3.88620	7.83302	0.		
(8) *M. vancouverensis*	10.38271	9.22482	8.75130	8.44063	6.01447	7.30795	7.21315	0.	
(9) *M. olympus*	9.61715	8.62819	7.47437	7.40201	5.39082	7.48480	6.03771	8.29043	0.

OCCASIONAL PAPERS

of the
MUSEUM OF NATURAL HISTORY
The University of Kansas
Lawrence, Kansas

NUMBER 84, PAGES 1-13 MARCH 27, 1980

A NEW MARSUPIAL FROG (HYLIDAE: *GASTROTHECA*) FROM THE ANDES OF ECUADOR

By

William E. Duellman[1] and Rebecca A. Pyles[2]

In a review of the marsupial frogs *(Gastrotheca)* of the Ecuadorian Andes, Duellman (1974) noted the occurrence of uniform green frogs on the Amazonian slopes of the Andes. Subsequent field work resulted in the acquisition of series of these green frogs, which are similar to *G. plumbea* (Boulenger) on the Pacific slopes of Ecuador and to *G. mertensi* Cochran and Goin from the eastern slopes of the Cordillera Central in southern Colombia. The latter species produces tadpoles (Cochran and Goin, 1970), whereas *G. plumbea* and the frogs on the Amazonian slopes have direct development of eggs into froglets. No other populations of Andean *Gastrotheca* are composed of uniform green individuals, although occasional green specimens of *G. marsupiata* (Dumeril and Bibron) and *G. monticola* Barbour and Noble lack dorsal markings (Duellman and Fritts, 1972; Duellman, 1974). Thus, we undertook an analysis of the Andean populations of green *Gastrotheca* in an attempt to determine their systematic status.

ANALYSES OF POPULATIONS

For purposes of analysis the frogs were assigned to three geographic populations—Amazonian, Pacific, and Colombian. Sixteen morphological measurements were obtained from each specimen.

[1] Curator, Division of Herpetology, Museum of Natural History; Professor, Department of Systematics and Ecology, The University of Kansas, Lawrence, Kansas 66045.

[2] Research Assistant, Division of Herpetology, Museum of Natural History, The University of Kansas, Lawrence, Kansas 66045.

Eleven of these, described in Duellman (1970), are, as follows: snout-vent length (SVL), tibia length, foot length, head length, greatest head width, eye diameter, tympanum diameter, interorbital distance, internarial distance, eyelid width, and snout length. Assessment of the lengths of the thumb and third finger follows Duellman (1974). Three additional measurements are: 1) orbit-jaw—the horizontal distance between the ventral margin of the orbit and the margin of the upper lip; 2) naris-jaw—the horizontal distance between the ventral margin of the external naris and the upper lip; and 3) width of disc on the third finger. All measurements were obtained to the nearest 0.1 mm with needle-tipped dial calipers.

A total of 25 external, descriptive characters also was assayed. Only ten of these are applicable to this analysis; the others are consistent among the three populations. Two descriptive characters—iris color and tympanum color—are consistent within populations. The remaining eight characters are variable; these are—labial stripe, flank color and pattern, posterior thigh pattern, anal region pattern, dorsal skin texture, and extent of webbing on fourth and fifth toes. Data for descriptive characters were recorded in a dichotomous fashion, i.e., presence or absence of a character or character state. Data obtained in this manner enables application of multivariate statistical analyses (Maxwell, 1961; Blackith and Reyment, 1971).

All statistical analyses were accomplished through the use of Biomedical Computer Programs (Dixon, 1975) at The University of Kansas Computation Center. Univariate statistics (BMDP2D), pairwise *t*-tests (BMDP3D), and one-way analysis of variance (BMDP1V) were obtained on all morphometric data. A cluster analysis of cases (BMDP2M) was used to verify group membership and to check for outliers in the data set. A stepwise discriminant analysis (BMDP7M) was then utilized to determine group separation based on morphometric and descriptive data. In univariate analyses, only adults separated by sex were used; in multivariate analyses, sexes were combined and juveniles were included.

Results of the ANOVA show that only eight morphometric characters (Table 1) have means that are significantly different ($P < 0.05$) among the three groups. In order to discern pairwise differences, two *t*-tests were generated. Because F_{max} tests indicated the presence of heteroscedasticity in some of the data, a *t*(separate) statistic was used to check the *t* values obtained from a pooled variance estimate. These results show that the means of the eight morphometric characters are significantly different ($P < 0.001$) between the Colombian and Amazonian populations. In the comparison of the Pacific and Colombian populations, all characters were significantly different ($P < 0.001$), except the width of the disc ($P = 0.36$). However, only five characters have significantly

different means ($P < 0.05$) between the Amazonian and Pacific populations; the three characters not different are head length ($P = 0.07$), eye diameter ($P = 0.16$), and tympanum diameter ($P = 0.30$).

The stepwise discriminant analysis is based only on those characters or character states that exhibited variation among the three populations. These include the morphometric characters and 33 descriptive character states. However, only two morphometric characters (tibia length and eye diameter) and eight descriptive character states (those pertaining to labial stripe, flank color, flank pattern, posterior thigh pattern, anal region pattern, dorsal skin texture, and extent of webbing on the fourth and fifth toes) contributed to the model. The best model for classification (jackknife classification 98.3% correct) included only labial stripe (present in Pacific population) and pale flank color (present in Amazonian populations).

In the discriminant analysis (see Fig. 1), canonical axis I discriminates between Pacific and Amazonian populations. Canonical coefficients vary from −7.97 for flank color to +4.73 for posterior thigh pattern; canonical correlation with axis I is 0.983. Canonical axis II contribution was found to be significant (eigenvalue = 16.01, $\chi^2_{113,1} = 165.76$, $P = 0.01$); correlation with axis II is 0.97. Canonical coefficients for axis II vary from −4.59 (extent of webbing on fourth toe) and −4.36 (flank pattern) to +8.47 (labial stripe). Canonical axis II discriminates between Pacific and Colombian populations.

The classification function of the discriminant analysis misidentified only three of 118 specimens (Fig. 1). Two specimens of the Pacific population were identified with the Colombian sample; one (KU 178528, a juvenile) lacks a labial stripe, and one (KU 164230) has a dark pattern on the flanks. One faded specimen (AMNH 17545) from the Pacific slopes appears to lack a labial stripe and dark flanks; therefore, it was classified with the Amazonian population. Nine additional specimens of the Colombian population were obtained subsequent to this analysis and form the basis for the description of coloration.

DESCRIPTION OF NEW SPECIES

The green *Gastrotheca* on the upper Amazonian slopes of the Cordillera Oriental in Ecuador obviously is distinct from other known species of the genus. No name is available for these frogs, for which we propose an epithet derived from the Greek *oros* meaning mountain and the Greek *phylax* meaning guard or watchman, used in the allusion that these frogs probably were watching in 1539 when a small band of Spanish Conquistadores led by Fran-

TABLE 1.—Univariate statistics for adults of three populations of *Gastrotheca*.

Characters	Sex	Amazonian ($n = 24\,♂\,♂, 26\,♀\,♀$) $\bar{x}$	Range	SD	Pacific ($n = 25\,♂\,♂, 15\,♀\,♀$) $\bar{x}$	Range	SD	Colombian ($n = 6\,♂\,♂, 6\,♀\,♀$) $\bar{x}$	Range	SD
Snout-vent	♀ ♀	53.74	47.6-59.1	3.25	56.65	42.1-61.0	3.77	60.92	56.2-65.7	3.16
	♀ ♀	59.34	50.8-74.0	5.94	64.16	58.2-73.0	4.24	68.40	62.5-72.6	3.37
Tibia	♂ ♂	26.29	21.7-29.5	1.64	28.29	22.6-32.3	1.92	31.65	30.9-33.3	0.86
	♀ ♀	29.80	25.0-37.0	3.40	32.35	30.2-34.5	1.42	35.53	33.7-38.2	1.70
Foot	♂ ♂	25.48	22.0-27.6	1.69	27.21	21.0-30.6	1.89	29.82	18.1-31.3	1.11
	♀ ♀	28.45	24.1-36.9	3.40	31.56	28.1-37.0	2.10	34.92	33.3-36.5	1.25
Head length	♂ ♂	18.20°	15.2-20.2	0.70	18.80	16.1-21.2	0.40	21.10	20.4-22.1	0.70
	♀ ♀	19.86°	17.5-23.8	0.95	21.47	19.4-25.2	1.60	23.57	22.9-24.2	0.43
3rd finger	♂ ♂	18.63	15.8-21.7	1.49	19.93	15.7-21.9	1.23	22.38	21.4-23.2	0.69
	♀ ♀	20.56	17.7-25.8	2.46	22.71	20.3-26.0	1.67	25.27	22.6-27.2	1.71
Disc	♂ ♂	2.94	2.4-3.6	0.32	3.47	2.5-3.9	0.28	3.40°	2.9-3.7	0.10
	♀ ♀	3.31	2.5-4.4	0.50	3.98	3.1-5.0	0.48	3.97°	3.6-4.3	0.27
Tympanum	♂ ♂	2.60°	2.8-4.7	0.37	2.69	1.9-4.4	0.25	3.34	3.2-3.4	0.05
	♀ ♀	2.78°	2.2-4.0	0.43	3.01	2.3-4.4	0.54	3.67	3.2-4.2	0.40
Eye diameter	♂ ♂	4.55°	3.9-5.6	0.23	4.34	3.1-5.0	0.20	5.72	5.5-5.9	0.17
	♀ ♀	5.03°	4.3-6.4	0.48	5.15	4.5-6.9	0.60	6.07	5.8-6.4	0.30

° Means not significantly different ($P > 0.05$) from those for Pacific population.

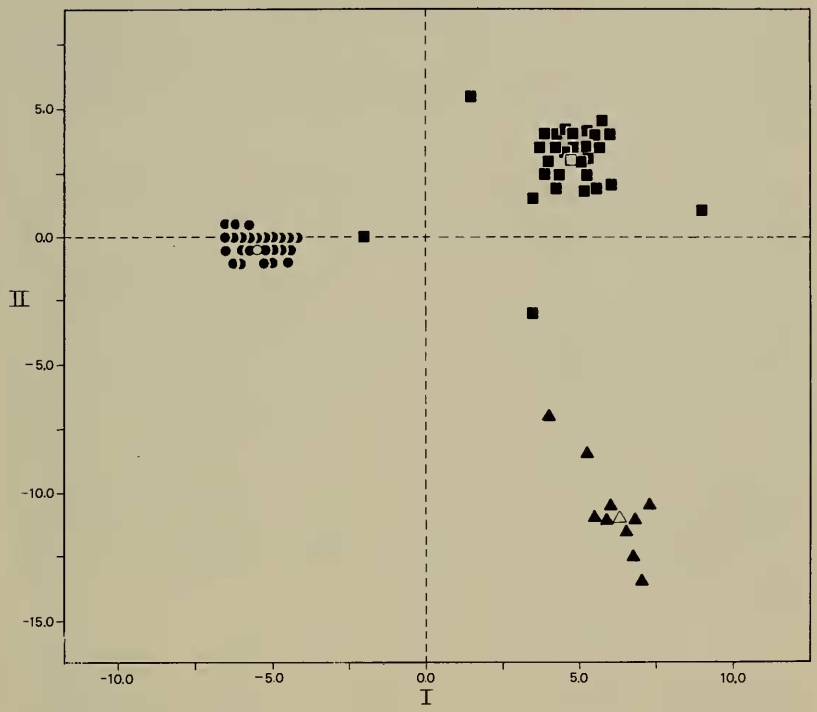

FIG. 1.—Multivariate plot of result of discriminant analysis of three populations of *Gastrotheca*. Circles = Amazonian population ($n = 56$); squares = Pacific population ($n = 50$); triangles = Colombian population ($n = 12$); open symbols = group means.

cisco de Orellana descended the Papallacta Valley on the expedition that resulted in the discovery of the Amazon.

Gastrotheca orophylax new species

Holotype.—University of Kansas Museum of Natural History (KU) 164243, a brooding female, from 11 km (by road) east-southeast of Papallacta, 2660 m, Provincia Napo, Ecuador, obtained on 22 March 1975 by Linda Trueb.

Paratypes.—All from upper Río Papallacta Valley, Provincia Napo, Ecuador: KU 164244, 178568 from the type locality; KU 117981 from 3 km E Papallacta, 2900 m; KU 155469-70, 164242 from 12 km E Papallacta, 2630 m; USNM 211207 from 2 km E Chalpi, 2730 m. Additional specimens, from the upper Chingual Valley, are not designated as paratypes.

Diagnosis.—*Gastrotheca orophylax* is a moderately large *Gastrotheca* (♂♂ attaining snout-lengths of 59.1 mm and ♀♀ 74.0 mm) with an uniform green dorsum and having direct development

of eggs into froglets. It is further characterized by the presence of smooth or areolate skin on the dorsum, skin not co-ossified with dermal roofing bones, uniform pale green flanks, uniform dark posterior surfaces of thighs, a dark bronze iris reticulated with black, a bronze-colored tympanum, and the absence of a labial stripe (Fig. 2).

Gastrotheca mertensi (Fig. 3) differs from *G. orophylax* by having more coarsely areolate or granular skin on the dorsum, dark flanks with or without pale spots, and a yellow tympanum. *Gastrotheca plumbea* differs from *G. orophylax* by having a pale labial stripe, uniformly brown flanks, uniformly pale posterior surfaces of the thighs, an olive-green iris, and a green tympanum. Some individuals of *G. plumbea* have dark flecks on the anterior and posterior surfaces of the thighs (Fig. 4), and others in life have a narrow, pale dorsolateral stripe (Fig. 5). Minor differences among at least some individuals of these species also exist in the extent of webbing on the fourth and fifth toes (least extensive in *G. mertensi*), color pattern of anal region (dark patch and/or pale anal stripe in *G. plumbea* and no pattern in others), and ventral coloration (dark with pale spots in some *G. mertensi* and uniformly pale in all others). *Gastrotheca mertensi* produces tadpoles, and *G. plumbea* has direct development of eggs into froglets.

Some individuals of two other Andean species of *Gastrotheca* are uniform green dorsally. Of these, *G. monticola* differs from *G. orophylax* by having a cream labial stripe, a bronze canthal stripe, dark spots on the flanks, pale dorsolateral stripe, and dark spots on the venter. Some *G. marsupiata* are uniform green dorsally but differ from *G. orophylax* by being much smaller (♂ ♂ attain snout-vent lengths of 41.6 mm and ♀ ♀ 46.5 mm) and by having a pale labial stripe, dark canthal stripe, and granular skin on the dorsum. Both *G. marsupiata* and *G. monticola* produce tadpoles.

Description of holotype.—Adult female with eggs in brood pouch; head wider than long; snout rounded in dorsal view and in profile; canthus angular; loreal region slightly concave; lips thin, rounded; nostrils nearly terminal on snout, slightly protuberant laterally; internarial region slightly depressed; interorbital area flat, much wider than eyelid; tympanic annulus indistinct; tympanum separated from eye by distance nearly equal to diameter of eye. Body robust; limbs moderately slender; ulnar tubercles absent; palmar tubercle diffuse; calcars absent; inner tarsal fold weak, present only distally; inner metatarsal tubercle elliptical, flat, visible from above; outer metatarsal tubercle absent; subarticular tubercles large, round; supernumerary tubercles large, flat, present only proximally; discs large, round; webbing absent between fingers; webbing formula of foot I2—2·II1.5—3III3—3IV3—1.5V. Skin on dorsum areolate; skin on belly and ventral surfaces of limbs coarsely granular; anal opening directed posteriorly at upper level of thighs,

lacking folds and tubercles; opening of pouch small, ⋀-shaped. Tongue cordiform; choanae small, round; prevomerine teeth 6-7 on abutting transverse processes between choanae.

Color (in preservative) of dorsum of head, body, and limbs, and anterior and posterior surfaces of thighs dull bluish gray; belly dull grayish cream; webbing dark gray.

Measurements of holotype in mm.—Snout-vent length 70.1, tibia 36.0, foot 34.4, head width 26.3, head length 23.5, interorbital distance 8.4, internarial distance 4.5, eyelid width 3.7, eye diameter 5.3, tympanum diameter 2.9.

Coloration in life.—The dorsal surfaces of the head, body, and limbs are bright emerald green. The flanks and margins of the upper lips are paler green. A bronze postorbital stripe is diffuse above the tympanum and disappears just posterior to the tympanum. There is a bronze suffusion on the outer edges of the forearms and feet and on the dorsal surfaces of the toes. The axilla, groin, and distal parts of the posterior surfaces of the thighs have a blue suffusion. The palmar and plantar surfaces are dark gray, and the ventral surfaces of the thighs are grayish bronze; the other ventral surfaces are pale green. In calling males the throat is bluish gray. The iris is deep bronze with black reticulations. The tongue is cream, and the lining of the mouth is pale blue.

Variation.—The known specimens of *Gastrotheca orophylax* are remarkably uniform in structure and coloration. Females are slightly larger than males (Table 1) but do not differ in coloration. The amount and intensity of blue suffusion in the groin and on the posterior surfaces of the thighs is slightly variable individually, as is the distinctness of the bronze postorbital stripe. Recently hatched young lack the blue and bronze colors and have a pale gray venter.

Distribution and ecology.—*Gastrotheca orophylax* is known from elevations of 2620-2910 m on the Amazonian slopes of the Cordillera Oriental in northern Ecuador and extreme southern Colombia (Fig. 6). Localities of occurrence are in the upper Río Papallacta Valley (2630-2900 m) and the upper Río Chingual Valley forming the border between Colombia and Ecuador (2620-2910 m). In both valleys, the frogs were found in disturbed upper montane forest that had been partially cleared for pastures. Viney bamboos *(Chusquea)* are dense in ravines, and large-leafed *Gunnera* (Haloragaceae) are abundant at edges of clearings. One individual was found beneath a stone by day; the others were collected at dusk and at night. Most were perched on leaves (1-2.5 m above the ground) of *Gunnera* and other large-leafed herbs.

Males have been observed calling in January, March, and July. The call is a moderately loud "bonk-bonk-bonk" repeated at intervals of 14-20 sec. Analysis of one recording (KU Tape 1224) shows that four calls have 3-6 ($\bar{x} = 4.5$) notes about 0.005 sec in duration with

FIG. 2.—*Gastrotheca orophylax*, KU 164243, holotype. ♀, 70 mm snout-vent length.

FIG. 3.—*Gastrotheca mertensi*, KU 181196, ♀, 75 mm snout-vent length.

FIG. 4.—*Gastrotheca plumbea,* KU 164229, ♀, 63 mm snout-vent length.

FIG. 5.—*Gastrotheca plumbea,* KU 142614, ♂, 54 mm snout-vent length.

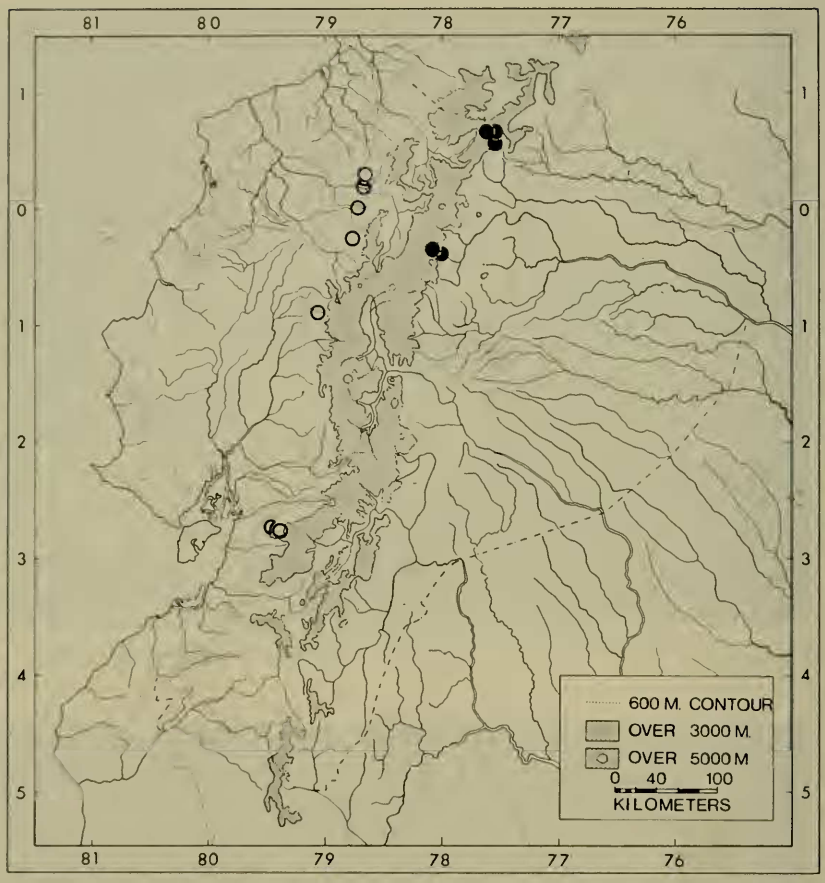

FIG. 6.—Distribution of *Gastrotheca orophylax* (dots) and *G. plumbea* (circles).

intervals of about 0.075 sec between notes; the fundamental frequency at about 500 Hz is dominant.

Brooding females have been found in March, May, June and July. Ten brooding females contained 12-32 ($\bar{x} = 21.4$) eggs having mean diameters of 5.19-7.23 ($\bar{x} = 6.13$) mm. Two brooding females collected on 22 June 1977 gave birth to froglets on 31 August and 25 September 1977. Ten newly born young have snout-vent lengths of 15.7-17.2 ($\bar{x} = 16.1$) mm.

DISCUSSION

Gastrotheca orophylax is a member of the *Gastrotheca plumbea* group, as defined by Duellman (1974). Of the seven species now recognized in that group, five (*G. cavia, lojana, monticola, psychrophila,* and *riobambae*) produce tadpoles that complete their de-

velopment in ponds, whereas *G. orophylax* and *G. plumbea* produce froglets. All of these species are essentially allopatric; *G. orophylax* and *G. riobambae* were both found at El Carmelo, Ecuador.

In addition to the same mode of reproduction and the similarities mentioned in the diagnosis, *G. orophylax* and *G. plumbea* are alike in having a bluish white cutaneous exudate, which is absent in other members of the group. Furthermore, the mating calls are similar and differ from the calls of the other species. Analysis of one recording of the call of *G. plumbea* (KU Tape 1036) reveals that the call consists of 3-6 ($\bar{x} = 4.3$) notes and that the call repetition rate is about 25 sec. Notes have a duration of about 0.007 sec, and the interval between notes is about 0.042 sec; the fundamental frequency at about 650 Hz is dominant.

Biochemical investigations of microcomplement fixation of albumins show that the immunological distance between *G. plumbea* and *G. orophylax* is 3 units and between *G. mertensi* and *G. orophylax* is 7 units (Linda Maxson, pers. comm.). According to Wilson et al. (1977), 100 units of albumin distance equals 55 million years of separation. Thus, immunological distances indicate a separation of *G. plumbea* and *G. orophylax* for about 1.6 million years. This places the separation in the Pleistocene, a time of continuing uplift of, and extreme climatic fluctuation in, the Andes (Simpson, 1975; Vuilleumier, 1971). Presumably a *G. orophylax-plumbea* stock existed at moderate elevations in the Andes of northern Ecuador. Either because of greater uplift of the mountains or vertical climatic-vegetational shifts, populations became isolated on opposite sides of the Andes. Now *G. orophylax* lives at elevations of 2620-2910 m on the eastern slopes and *G. plumbea* at similar elevations (2010-3085 m) on the western slopes (Fig. 6). *Gastrotheca mertensi* apparently is more distantly related to *G. orophylax* and *G. plumbea;* immunological evidence indicates a separation of about 3.8 million years, or late Pliocene.

Acknowledgments

Investigations on marsupial frogs have been conducted under grants from the National Science Foundation (DEB 74-01998 and DEB 76-09986). Many of the frogs were collected by David C. Cannatella, John D. Lynch, John E. Simmons, and Linda Trueb; we are also grateful to Eugenia del Pino for logistic support in Ecuador, Linda Maxson for information on the results of biochemical studies, Juan M. Renjifo for translating the Spanish summary, Debra K. Bennett for drawing figure 1, Linda Trueb for critical review of the manuscript, and the following curators for the loan of specimens and/or provision of facilities at their institutions: Alice G. C. Grandison, British Museum (Natural History) (BMNH); W. Ronald Heyer, National Museum of Natural History (USNM);